

On the Taxonomic Position, the Species and the Paleoecological Significance of the Genera

Eubora, *Toxosoma* and *Littoridina* (?)

in the Pliocene Pebas Formation of the Upper Amazon Region

(Gastropoda : Prosobranchia)

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(17 Text figures)

INTRODUCTION

THE TERTIARY SEDIMENTS of the Upper Amazon Basin, known as Pebas Formation (also named Iquitos Formation, *e.g.*, RUTSCH, 1952), contain a peculiar molluscan fauna which has been studied by GABB (1868), CONRAD (1871, 1874), H. WOODWARD (1871), BOETTGER (1878), ETHERIDGE (1879), DE GREVE (1938) and others. However, not all of the Mollusca have been studied satisfactorily. In this study it will be shown that the generic and even family position of some gastropods described from that formation has been incorrectly recognized; the taxonomic changes will affect interpretation of the ecological importance of the species concerned. Further, it will be pointed to the possibility of a biostratigraphical subdivision of the Pebas Formation based on different evolutionary levels of the species assemblages.

Formerly, the Pebas Formation was supposed to be of Oligocene age (*e.g.*, BOETTGER, 1878). More recently (*e.g.*, RUTSCH, 1952), it is placed into the Pliocene. An indication to this age is the occurrence of the Bivalve genus *Pachydon* Gabb, 1868, frequent in the Pebas Formation, in brackish water strata of Venezuela not older than Upper Miocene (with *Ammonia beccarii* (Linnaeus)).

The depositional environment has for a long time been considered to be brackish water because of the occurrence of the genus *Pachydon* which belongs to the marine bi-

valve family Corbulidae, and because of the occurrence of species of the families Neritidae, Hydrobiidae and Dreissenidae (inhabiting fresh and brackish waters), Lacunidae (marine to brackish waters) and Assimineidae (marine, supralittoral), while typical fresh water assemblages (with Planorbidae and Ampullariidae) were missing or rare. Therefore, a connection to the sea had been postulated which Rutsch supposed to have existed across Venezuela to the Caribbean (a distance of 3000 km). However, it will be shown that the species referred to Hydrobia, Assiminea and to the family Lacunidae probably do not belong to groups of marine or brackish water inhabiting animals, thus weakening the arguments supporting the brackish water character of the whole faunal assemblage.

MATERIAL

THE ENTIRE MATERIAL EXAMINED has already been published by different authors. It is preserved in the following institutions:

BM(NH): British Museum (Natural History), Department of Paleontology, London (WOODWARD, 1871 and ETHERIDGE, 1879).

NYSM: New York State Museum and Science Service, Albany, N.Y. (CONRAD, 1871).

- PIMUZ: Palaeontologisches Institut und Museum der Universität Zürich (DE GREVE, 1938).
 SMF: Natur-Museum Senckenberg, Frankfurt/M. (BOETTGER, 1878).
 UPP: Université de Paris, Collection de Paléontologie (COSSMANN, 1915).

ACKNOWLEDGMENTS

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PROVENANCE OF THE EXAMINED MATERIAL

The descriptions of the fossiliferous localities and the way that the fossils have taken from these localities may be compiled here (identical numbers refer to the same locality):

CONRAD, 1871:

Species: *Ebora crassilabra* Conrad, 1871 and *Ebora bella* Conrad, 1871 (now genus *Eubora* nom. nov.); Hauxwell collected, material sent to Conrad via Orton.

Localities: 1) Pebas, near the mouth of the Ambiyacu River, few shells; 2) South side of the Marañon River near Pichua, W of Cochaquinas, 48 km below Pebas; laminated and colored clays, "nearly the whole collection."

WOODWARD, 1871:

Species: *Ebora crassilabra* Conrad, 1871 (= *Eubora crassilabra* and *E. woodwardi* n. sp.), *Eubora bella* (Conrad, 1871) (not published by Woodward, but present in his collection); Hauxwell collected the material and sent it to Janson (London).

Localities: 1) near Pebas, Orton collected (?); 2) South side of the Marañon near Cochaquinas.

CONRAD, 1874:

Species: *Ebora crassilabra* Conrad, 1871 (now *Eubora*, nom. nov.), *Toxosoma eboreum* Conrad, 1874 and *Lio-*

soma curta Conrad, 1874 (both conspecific); Steere collected and sent the material to Eug. W. Hilgard.

Localities: 3) "near Tabatinga," blue clay with seams of dirty coal; 1) Pebas, 1.6 km off the mouth of the Ambyacu River, 18-21 m above the water level. Section: 8' clay, red and white, and sand (= soil and alluvial formations); 20' blue clay, with 4' of fossiliferous beds; 6" coal seam; 15' blue clay, with 3' of fossiliferous beds; 4) Old Pebas, ca. 3.2 km below the mouth of the Ambyacu River, at the water level; 5) Pichana, ca. 24 km away from the mouth of the Ambyacu River.

BOETTGER, 1878:

Species: *Lacuna (Ebora) crassilabris* (Conrad) Boettger, 1878 (= *Eubora crassilabra* Conrad, 1871), *L. (E.) bella* (Conrad, 1871), *L. (E.) bella semisculpta* Boettger, 1878 (both = *Eubora bella* s. str.), *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874). Juan Hauxwell collected the material, which Boettger received via P. Abendroth and W. Kobelt.

Localities: the same as of Conrad, 1871 and Woodward, 1871.

C. B. BROWN, 1879, and ETHERIDGE, 1879:

Species: *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874), *Assimineea crassa* Etheridge, 1879 and *Hydrobia dubia* Etheridge, 1879 (both = *Littoridina? crassa*).

Locality: Brazil, "cliff of the Javary River, at Canama, 200 yards above the little settlement of that name, and some 50 miles up, in a straight line, from the mouth of the Javary." Clay, bluish and greenish-blue, in part with calcareous concretions, lignite seam.

COSSMANN, 1915 figured and described material sent to him by Boettger.

GREVE, L. DE, 1938:

Species: *Lacuna (Ebora) crassilabris* (not of Conrad, 1871, comprises *Eubora woodwardi* n. sp., *E. grevei* n. sp., *E. pygmaea* n. sp.), *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874).

Locality: Cliff of the Itaya River near the telegraph station of Iquitos.

TAXONOMIC TREATMENT

Legend for the synonymy list of the species:

- v: the original material was examined (at least partly).
 *: a new name of the species name group is validly published with this reference.
 ?: doubtful synonymy.

Eubora Kadolsky, new name

Type species, *Ebora crassilabra* Conrad, 1871

- 1871 *Ebora* CONRAD, p. 194 (type by monotypy: *Ebora* (*Ebora*) *crassilabra* Conrad, 1871) (not *Ebora* Walker, 1867, p. 415).
 1871 *Ebora* (*Nesis*) CONRAD, p. 194 (type by monotypy: *Ebora* (*Nesis*) *bella* Conrad, 1871) (not *Nesis* MULSANT, 1850: 67, not STÅL, 1860: 67)

Diagnosis: Shell medium-sized, ovate-conical; two embryonic whorls with deep sutures and fine growth lines; the first one coiled nearly in a plane; the next very slowly, the succeeding more rapidly descending; later whorls about 4, regularly increasing, sutures only moderately deepened; surface sculptured with growth lines, very fine incised spiral lines and in some forms with strong spiral keels. Growth lines and outer lip opisthocyrt in its adapical portion, abapically of the periphery protruded and prosocline, thus forming an inverted "S". Outer lip often reflected and thickened; aperture isometric, angular at the junction of parietal and palatal margins, and at the junction of columellar and parietal margins and truncated abapically by a siphonal (?) notch. Umbilicus closed, but a pseudumbilicus may be formed by the strongly thickened and elevated columellar margin. This pseudumbilicus is surrounded by an umbilical ridge which ends in the siphonal (?) notch. Umbilical ridge, pseudumbilicus and siphonal (?) notch not present in juveniles.

Former work on the relationships of the genus: CONRAD (1871; 1874) did not indicate an opinion on the taxonomic position of the genus. WOODWARD (1871) and BOETTGER (1878) assumed a relationship with the genus *Lacuna* Turton, 1827; Boettger even considered *Ebora* Conrad to be a subgenus of *Lacuna*. This view has been maintained in principle up to today, with the alteration that *Ebora* Conrad, 1871 was synonymized with *Pseudocirsope* Boettger, 1907 and suppressed because of its homonymy with *Ebora* Walker, 1867. So did COSSMANN (1915) and WENZ (1939). Because of the assumed synonymy with *Pseudocirsope*, no substitute name was proposed for the preoccu-

pied *Ebora* Conrad. Contrary to these authors, PILSBRY (1944) maintained *Ebora* as a distinct genus and indicated a relationship to *Potamolithus* Pilsbry, 1911, family Amnicolidae.

The type species of *Ebora* Conrad is sculptured with growth lines only, while *E. bella* Conrad exhibits several strong spiral keels. Upon this character, Conrad founded the subgenus *Nesis* which is preoccupied as well as is *Ebora* Conrad. BOETTGER (1878) and probably WENZ (1939) did not consider the presence of spiral keels to be of subgeneric importance, but WOODWARD (1871) did so. COSSMANN (1915) placed *Eubora bella* even into the genus *Fossarus* Philippi which has only very remote relationships to *Lacuna* (*Pseudocirsope*) where Cossmann placed *E. crassilabra*. The spiral keels are here considered to be of minor taxonomic significance, as they display a high interspecific variability (compare *Eubora woodwardi*, *E. grevei* and *E. crassilabra*).

Discussion of possible relationships of the genus *Eubora*a) *Cirsope* (*Pseudocirsope*) O. Boettger, 1907

The attribution of *Eubora* to *Pseudocirsope* is now considered to be erroneous as based on convergence in shell characters. Distinguishing features are:

1) The growth lines of *Pseudocirsope* are straight, slightly prosocline to orthocline, and are not protruded abapically, while those of *Eubora* are opisthocyrt in its adapical portion, grading into prosocline ones in its abapical portion.

2) *Pseudocirsope* has a true though small umbilicus while *Eubora* has only a pseudumbilicus formed by the elevation of the thickened columellar margin in adults.

3) *Pseudocirsope* has in general a small funicle while *Eubora* has none.

4) *Pseudocirsope* has in general conspicuous spiral striae while *Eubora* has extremely delicate spiral lines only and in some cases spiral keels.

5) Umbilical ridge and siphonal notch are present in *Pseudocirsope* throughout ontogeny, while in *Eubora* they make their appearance in late ontogenetic stages and increase in strength with increasing age.

The homoeomorphous features are the general shape of the shell and of the aperture and the presence of an umbilical ridge and of a siphonal (?) notch. However, as the shape of the growth lines is a tool to distinguish higher

taxonomic categories (families, superfamilies), the growth lines indicate that *Eubora* and *Pseudocirsope* must belong to different families or even superfamilies.

As pointed out by KADOLSKY (1973), the growth lines in the families Littorinidae and Lacunidae of the superfamily Littorinacea are invariably prosocline to orthocline. In that paper, the taxon *Pseudocirsope* has been removed from the genus *Lacuna* and subgenerically attributed to the genus *Cirsope* Cossmann, 1888 (s.l.), which in a restricted sense formerly has been treated as a subgenus of *Lacuna* as well as *Pseudocirsope*. The relationship between *Cirsope* and *Lacuna* appears not to be very close, and in future *Cirsope* may be classified anywhere in the Prosobranchia Mesogastropoda. Any classification differing from that in the family Lacunidae, however, would not affect the above statement that *Eubora* and *Pseudocirsope* are homoeomorphs.

b) Genera from the Pebas Formation

Tropidebora Pilsbry, 1944: This genus is almost certainly related to *Eubora*, as it differs mainly in possessing a strong peripheral keel and a blunt shoulder on the adapical portion of the whorls. It has a siphonal (?) notch, a pseudumbilicus, a ridge contouring the umbilical area and a thick parietal callus, which are also characteristic of *Eubora*.

Toxosoma Conrad, 1874: Differs mainly by the presence of a supracolumellar fold and also by a more protruded outer lip in adult specimens. By all other characters a close relationship to *Eubora* is proven.

c) *Potamolithus* Pilsbry, 1911

The type species, *P. rushi* Pilsbry, 1911, has no apertural notch although there is a ridge surrounding the umbilical area. As in the juvenile stage the columella is "semicircular," while it is narrow in *Eubora*, this feature may be homoeomorphous. However, many other species placed by PILSBRY (1911) in *Potamolithus* have an apertural notch and also a pseudumbilicus. These species may in fact be related to *Eubora*; at present the nominal genera are separated as the type species of *Potamolithus* lacks essential characters of *Eubora*, and it cannot be completely ruled out that PILSBRY (*op. cit.*) assembled a heterogeneous community under the heading of *Potamolithus*, or that features in common are homoeomorphous. For example, species of both genera may have spiral keels, but their pattern differs: *Eubora* may have 7 keels which may become reduced to 3 or to nil, while *Potamolithus* species may have 1-3 strong keels.

d) *Lithococcus* Pilsbry, 1911

Although superficially similar to keeled *Eubora* species by its sculpture, *Lithococcus* lacks an apertural notch and is therefore unrelated to *Eubora*.

e) *Mexithauma* Taylor, 1966

As in *Lithococcus*, *Mexithauma* resembles *Eubora* by the presence of spiral keels. However, *Mexithauma* has strictly prosocline growth lines, no apertural notch, a much less developed pseudumbilicus (only in largest specimens) and no umbilical ridge.

Eubora crassilabra (Conrad, 1871)

(Figures 3-4, cf. Figure 5)

- v*1874 *Ebora* (*Ebora*) *crassilabra* Conrad, p. 194; pl. 10, fig. 14; two localities mentioned: nearly the whole collection was obtained from "nearly 30 miles below Pebas, on the south side of the Marañon, at Pichua, just west of Cochaquinas"; minor collections "at Pebas, near the mouth of the Ambiyacu."
Holotype: NYSM 9194, 9.0 : 6.5 mm, here Figure 3, probably from the first-mentioned locality; no paratypes preserved.
- v 1871 *Ebora crassilabra* - Woodward, p. 102 (near Cochaquinas and near Pebas) (partly; fig. is *Eubora woodwardi* n. sp.)
- ? 1874 *Ebora crassilabra* - Conrad, p. 32, pl. 1, fig. 9 (no locality given; figure may be *Eubora woodwardi* n. sp.)
- v*1878 *Lacuna* (*Ebora*) *crassilabris* - Boettger, p. 494, pl. 13, figs. 1a-d ("Pebas," same provenance as the type material).
- 1915 *Lacuna* (*Pseudocirsope*) *crassilabris* - Cossmann, p. 102.
- 1944 *Ebora crassilabris* - Pilsbry, p. 150.

Diagnosis: Shell elongate ovate-conical; sculptured with growth lines and very delicate spiral lines only. Umbilical ridge and siphonal notch distinct. Outer and inner lip markedly thickened; inner lips raised over the body whorl, columellar lip forming a pseudumbilicus; outer lip expanded.

Relations: Most closely allied is *Eubora woodwardi*, n. sp., which differs from *E. crassilabra* in being somewhat smaller, relatively broader ovate-conical (for measurements see Figures 1, 2) and with weaker umbilical ridge, weaker siphonal (?) notch and lesser thickened lips.—*Eubora pygmaea* n. sp. has half the size of *E. crassilabra*, but is in its shape and apertural characters very similar;

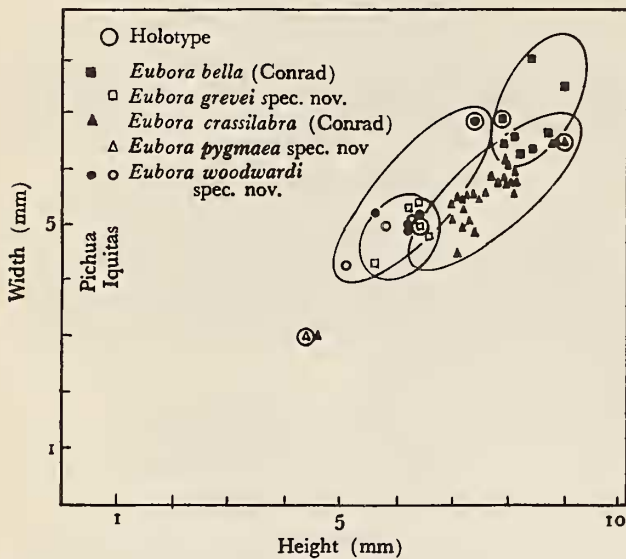


Figure 1

Crossplot height:width of the available material of the species of *Eubora* Kadolsky, nom. nov.

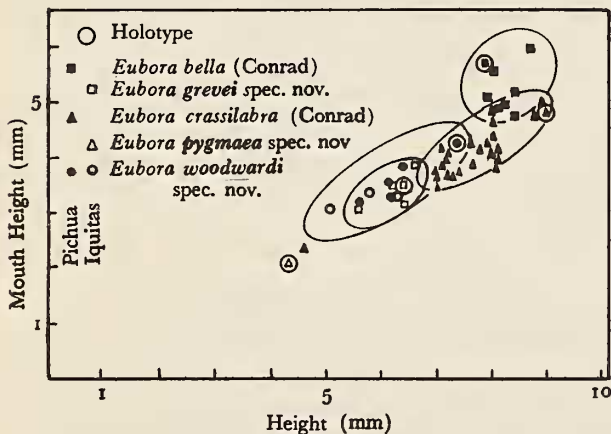


Figure 2

Crossplot shell height:mouth height of the available material of *Eubora* Kadolsky, nom. nov.

juvenile specimens of *E. crassilabra* (cf. Figure 5) differ in being completely devoid of umbilical ridge, siphonal (?) notch and pseudumbilicus.—*Eubora bella* (Conrad) and *E. grevei*, n. sp. are broader in shape and provided with spiral keels.

Nomenclatorial Remarks: Two closely related species occur at Cochaquinas which hitherto have been confused: *Eubora crassilabra* (Conrad) and *E. woodwardi*, n. sp. Unfortunately, the original figure of *E. crassilabra* is inadequate, while the figure of WOODWARD published in the same year (1871) is excellent but represents the latter-named species. The holotype of Conrad's species, however, restricts the meaning of the species name to the larger, more conical and more slender form, which furthermore is much more frequent at the type locality.—*Lacuna crassilabris* Boettger, 1878 is an unjustified emendation of the specific name.

Material and localities: Probably all material from Pichua near Cochaquinas (NYSM 9194, holotype; BM(NH) GG 19830/1-25, WOODWARD, 1871; SMF XII. 2918a, 1 spec., BOETTGER, 1878).

Eubora woodwardi Kadolsky, spec. nov.

(Figures 6-8)

v 1871 *Eubora crassilabra* – Woodward, p. 102 (part), pl. 5, figs. 1a, b (near Cochaquinas and near Pebas) (not Conrad, 1871).

v 1938 *Lacuna (Eubora) crassilabris* – DE GREVE, p. 70-72 (part), pl. 5, fig. 22 (Iquitos) (not *crassilabris* Boettger, 1878; not figs. 19, 20, 21, 23 which are *Eubora grevei* n. sp.).

Holotype: BM(NH) GG 19831/1, figured by WOODWARD, 1871, pl. 5, fig. 1 and this paper, Figure 6. Height, 7.4 mm; width, 6.9 mm.

Type Locality (hereby restricted): Pichua W. Cochaquinas, Upper Amazon Basin, Peru.

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by the broadly ovate-conical shape of the shell, the absence of spiral keels and the development of umbilical ridge, pseudumbilicus, siphonal notch and thickening of lips less pronounced than in the closely related *E. crassilabra*, particularly in specimens remaining smaller than *E. crassilabra*.

Relationships: Juvenile specimens of *Eubora crassilabra* cannot be distinguished from *E. woodwardi*, as apertural and siphonal properties of *E. crassilabra* as well as of *E. woodwardi* are late ontogenetic features and the shell proportions of juveniles are very similar (see crossplots height/width and height/mouth height, Figures 1, 2).—*Eubora grevei* n. sp. is very closely related, too, as its shell

shape is nearly identical. It is, however, easily distinguished by the presence of spiral keels.

Variability: For variability of the height, width and mouth height see Figures 1 and 2; the specimens of Iquitos are generally smaller than those of Pichua.

Localities and Material: Pichua W of Cochaquinas (BM(NH) GG 19831, holotype and 4 paratypes); Iquitos, Itaya River cliff near the telegraph station (PIMUZ, 3 paratypes, Figures 7 and 8 of this paper); all Pebas Formation, (?) Pliocene.

Eubora bella (Conrad, 1871)

(Figures 9-10)

- v*1871 *Ebora (Nesis) bella* CONRAD, p. 194, plt. 10, fig. 17 (localities mentioned: nearly the whole collections were obtained "nearly 30 miles below Pebas, on the south side of the Marañon, at Pichua, just west of Cochaquinas"; minor collections "at Pebas, near the mouth of the Ambiyacu." Holotype NYSM 9193, in this paper Figure 9, probably from the first-named locality. No paratypes preserved).
- v 1871 *Ebora (Nesis) bella* - WOODWARD, p. 102-103, plt. 5, fig. 3 (copy of Conrad's fig. 17).
- v 1878 *Lacuna (Ebora) bella* - BOETTGER, p. 494-495, plt. 13, fig. 3 ("Pebas," same provenance as Conrad's material).
- v*1878 *Lacuna (Ebora) bella* var. *semisculpta* Boettger, p. 495, plt. 13, fig. 2 (Holotype: SMF XII 2920a, in this paper Figure 10; probably from Pichua W. of Cochaquinas.)
- 1915 *Fossarus bellus* - COSSMANN, p. 88.
- 1938 *Lacuna (Ebora) bella* - DE GREVE, p. 72-73.

Diagnosis: A species of *Eubora* characterized by the broad ovate-conical shape, the relatively large size and the presence of 6 to 7 spiral keels of which 2 to 3 remain uncovered by the succeeding whorl.

Relationships: *Eubora grevei* n. sp. is certainly the nearest ally as it displays 3 spiral ribs which are equivalent to the 3 adapical keels of *E. bella*. However, *E. grevei* remains smaller, the apertural and siphonal (?) characters being less developed. The "variety" *semisculpta* Boettger, 1878, was founded on a single specimen with weaker spiral keels, but this specimen is no intermediate to *E. grevei* as the keels are still stronger developed than in *E. grevei* which further lacks the two umbilically positioned ones and the adapically positioned one. The latter, however, is not even present in all specimens of *E. bella*.

Variability: For variability of shell height, width and mouth height see crossplots Figures 1 and 2. The spiral keels vary in strength, the most adapically positioned one (Figure 10) is often absent.

Localities and Material: Pichua W. of Cochaquinas, Pebas Formation, Pliocene (NYSM 9193, holotype; BM(NH) GG 19832, 5 specimens, Woodward collection, although WOODWARD (1871) stated to possess no specimens; SMF XII 2919a-20a, 2 specimens, Boettger collection: *bella* s. str. and *bella semisculpta* Boettger, holotype).

Eubora grevei Kadolsky, spec. nov.

(Figure 11)

- v 1938 *Lacuna (Ebora) crassilabris* - DE GREVE, p. 70-72 (part), plt. 5, figs. 19, 20, 21, 23 (not fig. 22 which is *E. woodwardi* n. sp.) (not *Ebora crassilabra* Conrad, 1871, nor *Lacuna (Ebora) crassilabris* Boettger, 1878).

Holotype: PIMUZ J/4, Figure 11 of this paper; height, 6.4 mm; width, 5.0 mm; coll. de Greve, no. 266.

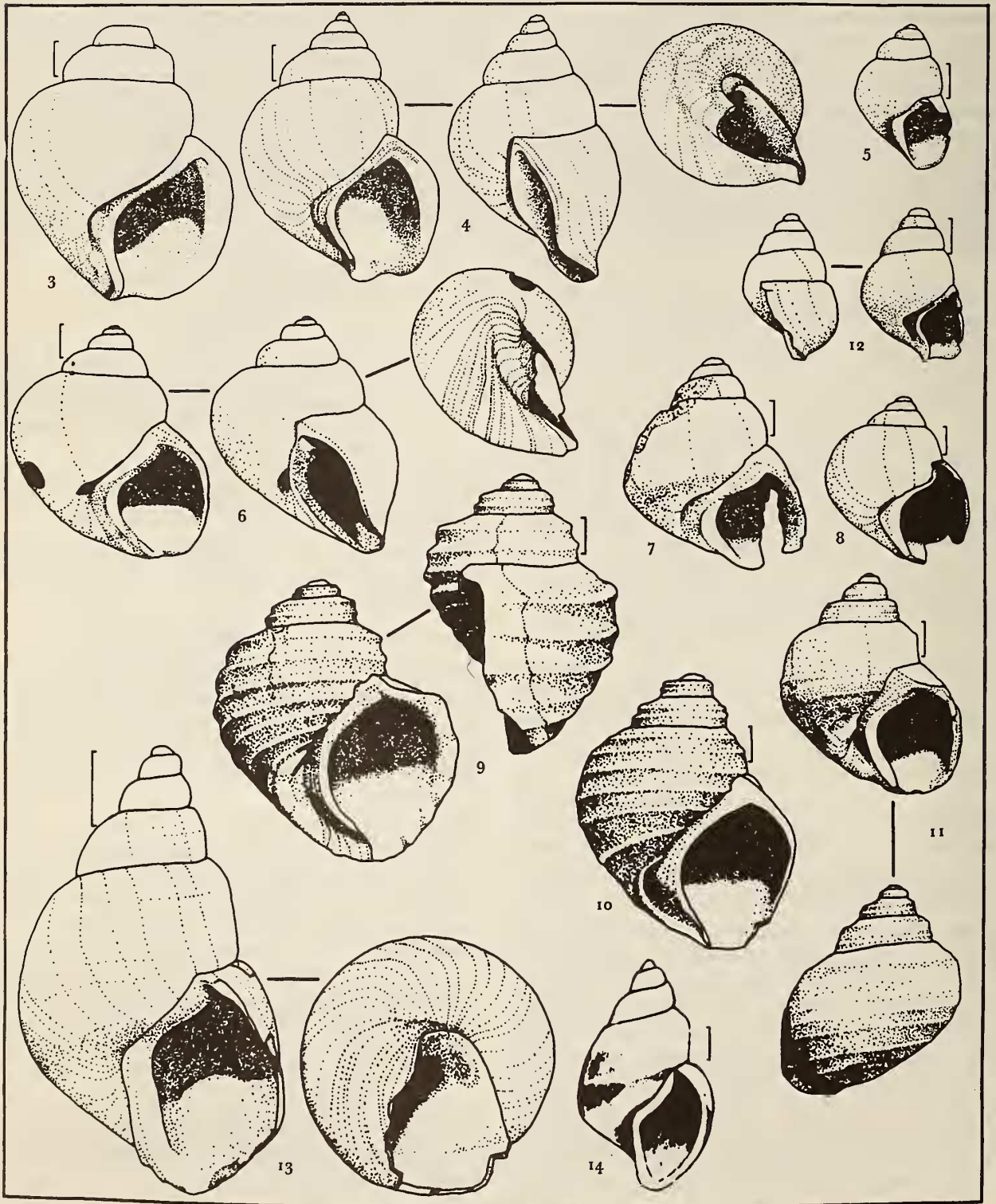
Type Locality: Peru, Upper Amazon Basin, Iquitos, Itaya river cliff near the telegraph station, locality VI of DE GREVE, 1938.

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by the broadly conical-ovate shape of the shell, the presence of three spiral ribs two of which remain uncovered by the succeeding whorls, the apertural characters and the size similar to that of *E. woodwardi*, but less developed than in *E. crassilabra*.

Relationships: The species occurs together with *E. woodwardi*, in Iquitos, and is distinguished mainly by the presence of spiral ribs. The shell of *E. grevei* seems to be somewhat more slender than that of *E. woodwardi*, but the crossplots Figures 1 and 2 show overlaps indicating that this difference derived from few specimens may not be significant.—*E. bella* has two more keels on the umbilical side and occasionally one more near the suture; all keels are much stronger developed, the size of the shell is larger and the apertural and siphonal (?) properties are stronger developed than in *E. grevei*. Doubtless *E. grevei* and *E. bella* are directly related to each other.

Localities and Material: Pebas Formation, Pliocene: Iquitos (PIMUZ, holotype and 6 paratypes, collection de Greve, nos. 263-270).



Eubora pygmaea Kadolsky, spec. nov.

(Figure 12)

v 1938 *Lacuna (Ebor) crassilabris* - DE GREVE, p. 70-72
(part, figs. excluded; not *crassilabra* Conrad, 1871,
nor *crassilabris* Boettger, 1878).

Holotype: PIMUZ J/2, Figure 12 in this paper; height 4.8 mm, width 3.7 mm; collection de Greve no. 249.

Type Locality: Peru, Upper Amazon Basin, Iquitos, Itaya river cliff near the telegraph station.

(← on facing page)

Figures 3 to 14

Eubora crassilabra (Conrad, 1871)

Figure 3: Holotype, NYSM 9194, probably from the southern bank of the River Marañon at Pichua, near Cochaquinas
Figure 4: BM(NH) GG 19830/1, probably the same locality, Woodward collection

Eubora cf. *E. crassilabra* (Conrad, 1871)

Figure 5: BM(NH) GG 19836, probably the same locality as of Figs. 3 and 4; juvenile specimen, may be *E. woodwardi*

Eubora woodwardi Kadolsky, spec. nov.

Figure 6: Holotype, BM(NH) GG 19831/1. Southern bank of the River Marañon at Pichua, near Cochaquinas. WOODWARD, 1871: plt. 5, fig. 1

Figure 7: Paratype, PIMUZ J/3, Itaya River cliff near Iquitos; collection de Greve no. 262

Figure 8: Paratype, PIMUZ J/5, collection de Greve no. 268; same locality as Figure 7

Eubora bella (Conrad, 1871)

Figure 9: Holotype, NYSM 9193, probably from the southern bank of the River Marañon at Pichua, W of Cochaquinas

Figure 10: Holotype of *Lacuna (Ebor) bella semisculpta* Boettger, 1878; probably same locality, SMF XII 2920a

Eubora grevei Kadolsky, spec. nov.

Figure 11: Holotype, PIMUZ J/4, collection de Greve no. 266; Itaya River cliff near Iquitos

Eubora pygmaea Kadolsky, spec. nov.

Figure 12: Holotype, PIMUZ J/2, collection de Greve no. 249; same locality as Figure 11

Littoridina? *crassa* (Etheridge, 1879)

Figure 13: Lectotype, BM(NH) GG 19833/1; Javary River cliff near Canama

Figure 14: Lectotype figure of *Hydrobia dubia* Etheridge, 1879: plt. 7, fig. 11; same locality as Figure 13

All fossils are from the Pebas Formation, Pliocene, of the Upper Amazon Basin. The scales represent 1 mm

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by its very small size (half of *E. crassilabra*), conical shape of the spire, lack of sculpture, weakly curved growth lines being prosocline rather than like an inverted "S"; apertural characters diagnostic for the genus distinctly developed.

Relationships: The new species is founded on a single specimen erroneously determined as *Eubora crassilabra* by de Greve. From this species, however, it is easily distinguished by its size, having only nearly half the height of *E. crassilabra* but having 1 more whorl than juvenile specimens of the latter (cf. Figure 5) which, moreover, are devoid of the apertural and siphonal (?) properties of the adult specimens. The growth lines are also different, being more weakly curved in *E. pygmaea*. — *Eubora woodwardi*, *E. grevei* and *E. bella* (Conrad) are much larger, too, and different in their shape, being more broadly ovate-conical. The two latter-named species have spiral ribs or keels.—*Littoridina?* *crassa* (Etheridge) is of comparably small size, but devoid of umbilical ridge, pseudumbilicus, siphonal (?) notch and elevated columellar margin, the sutures are more deepened and a weak and irregular spiral ornamentation can be seen.

Material: Only the holotype.

Littoridina? *crassa* (Etheridge, 1879)

(Figures 13 - 14)

v* 1879 *Assimineia crassa* ETHERIDGE, p. 86-87 (lectotype designated herein, fig. 13, BM(NH) GG 19833/1, Brazil, Canama, Pebas Formation).

*1879 *Hydrobia dubia* Etheridge, p. 86; plt. 7, fig. 11 (lectotype figure, here redrawn Figure 14; Brazil, Canama, Pebas Formation).

Diagnosis: A species referred with some doubt to the genus *Littoridina*, as the rhomboidal aperture and the stepped contours of the whorls are somewhat atypical for that genus. The species is characterized by its conical shape, relatively small size, deeply incised sutures and the slope of the whorls strongly rounded in the adapical portion, then only slightly convex to straight and steeply sloping, thus causing step-like contours of the spire; sculptured with growth lines and irregular spiral striae.

Relations and Generic Attribution: The species is in general characters similar to juvenile *Eubora crassilabra*, especially in missing the apertural features characteristic of the genus *Eubora* (Figure 5); the species, however, are distinguished by the shape of the spire being conical in

L.? *crassa* instead of being ovate-conical in *E. crassilabra*, the angle between columellar and parietal lip being smaller, and the whorls more evenly rounded in *E. crassilabra*.

The shells of the genus *Hydrobia* Hartmann, 1821 are more slender, the angle between columellar lip and parietal lip is much more rounded and the whorls are more evenly rounded. *Assimineea* Fleming, 1828 has a similar broadly conical shape, but the growth lines are orthocline, not curved like an inverted "S".

Synonymy and Types: The lectotype figure of "*Hydrobia dubia*" Etheridge is so similar to the lectotype of "*Assimineea*" *crassa* Etheridge that they have to be considered to be conspecific. The measurements differ little (Etheridge's figure of "*Hydrobia dubia*": height ca. 6.7 mm; lectotype of *crassa*: height 6.0 mm) but this difference is not significant. No syntypes of *Hydrobia dubia* Etheridge are present in the British Museum (Natural History). To explain this lack, one might assume that the types of *Hydrobia dubia* were confounded with those of *Assimineea crassa*. However, Etheridge stated to possess two specimens of his *Hydrobia dubia*, but the syntypic material of *Assimineea crassa* consists of three specimens. Thus, at least one specimen cannot belong to the syntypes of *Hydrobia dubia* but could be a syntype of *Assimineea crassa*. Unfortunately, Etheridge did not indicate the number of specimens of his *Assimineea crassa*. Of the three specimens of the British Museum, one was loose while two were pasted on a pasteboard. As a confusion of the syntypes cannot be proven, all three specimens are considered to be syntypes of *Assimineea crassa* Etheridge, 1879. Preference is given to the specific name *crassa* Etheridge, 1879 over *dubia* Etheridge, 1879 because of the existence of original material.

Locality and Material: Pebas Formation, Pliocene: Brazil, Canama, cliffs of the Javary river (BM(NH) GG 19833: lectotype and 2 paratypes of *Assimineea crassa* Etheridge, 1879).

Genus *Toxosoma* Conrad, 1874

- 1874 *Toxosoma* CONRAD, p. 31. Type by monotypy: *Toxosoma eboreum* Conrad, 1874.
 1874 *Liosoma* CONRAD, p. 31. Type by monotypy: *Liosoma curta* Conrad, 1874. (Not *Liosoma* Brandt, 1835, nor Fitzinger, 1843, nor Agassiz, 1846).
 1878 *Pseudolacuna* BOETTGER, p. 495-496. Type by monotypy: *Pseudolacuna macroptera* Boettger, 1878.

1879 *Alycaedonta* ETHERIDGE, p. 85 (footnote) (nomen nudum, published in synonymy of *Pseudolacuna* Boettger, 1878).

Diagnosis: Shell similar to that of *Eubora*, but with a supracolumellar fold, and occasional thickenings on the columellar and parietal lips and on the palatal shell wall; outer lip thickened and strongly expanded over the preceding whorl; growth lines distinctly opisthoclyt in the apical portion and prosoclyt in the abapical portion.

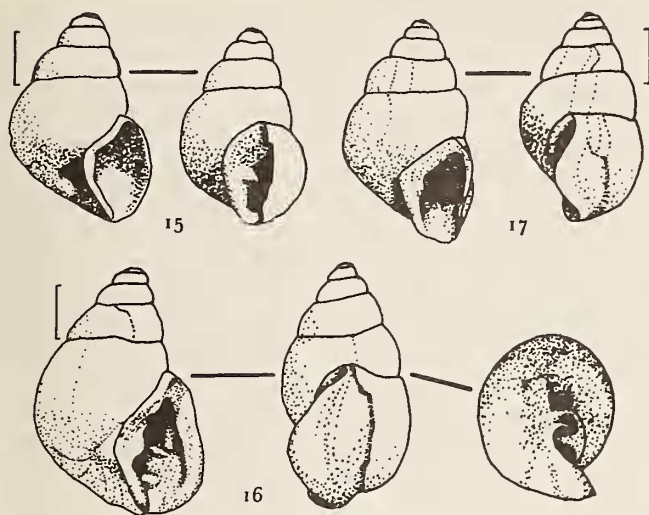
Relationships: *Toxosoma* Conrad is closely related to *Eubora*, but the above mentioned characters justify a separation on the genus level. The genus *Toxosoma* Conrad is proposed to be placed tentatively in the family Hydrobiidae s. lat. (superfamily Rissoacea) instead of family Lacunidae (superfamily Littorinacea) for the same reasons as given for the genus *Eubora*.

Toxosoma eboreum Conrad, 1874

(Figures 15-17)

- *1874 *Toxosoma eborea* CONRAD, p. 31; pl. 1, fig. 7 (localities mentioned p. 26: Tabatinga, Pebas, Old Pebas and Pichana, collected by Steere; holotype in Academy of Natural Sciences of Philadelphia, no. 161152 (see PILSBRY, 1944)).
 *1874 *Liosoma curta* CONRAD, p. 31; pl. 1, fig. 8 (for localities see *Toxosoma eboreum* Conrad).
 v*1878 *Pseudolacuna macroptera* BOETTGER, p. 496, pl. 13, figs. 14-15 ("Pebas," J. Hauxwell collected; localities according to CONRAD, 1871; Pichua W. of Cochiquinas ("nearly the whole collection") and mouth of the Ambiyacu river near Pebas (few specimens); holotype, UPP, here Figure 15; no syntypes in Boettger's collection, SMF).
 v 1879 *Pseudolacuna macroptera* - ETHERIDGE, p. 85, pl. 7, fig. 12 (Canama).
 v 1915 *Pseudolacuna macroptera* - COSSMANN, p. 107, pl. 12, figs. 27-30 (holotype, here Figure 15; sent by Boettger to Cossmann; UPP, Cossmann collection no. 15485).
 v 1938 *Pseudolacuna macroptera* - DE GREVE, p. 74-76; pl. 5, figs. 17, 18, 24-29 (Iquitos).
 v 1939 *Pseudolacuna macroptera* - WENZ, p. 514, fig. 1347 (copy Boettger, 1878).
 • 1944 *Toxosoma eboreum* - PILSBRY, p. 151, fig. 3a, b (type).
 • 1969 *Toxosoma eborea* - PARODIZ, p. 121.

Diagnosis: Shell small, spire irregularly conical to ovate conical, sculptured with fine growth lines only; strong



Figures 15 to 17

Toxosoma eborea Conrad, 1874

Figure 15: Holotype of *Pseudolacuna macroptera* Boettger, 1878; UPP, collection Cossmann no. 15485. Probably from the southern bank of the River Marañon at Pichua, W of Cochaquinas

Figure 16: BM(NH) GG 19834/1, collection Etheridge; Javary River cliff near Canama

Figure 17: PIMUZ J/1, collection de Greve no. 246A; Itaya River cliff near Iquitos

All fossils are from the Pebas Formation, Pliocene, of the Upper Amazon Basin. The scales represent 1 mm

supracolumellar fold invariably present; thickenings on the columella, on the parietal wall and on the palatal wall may be developed, particularly in gerontic stages; in adults parietal and columellar lip strongly thickened and elevated, causing a deep pseudumbilicus umbilical ridge becoming acute, outer lip either thickened, expanded, tending to become straight to concave in the middle portion, and ascending on the penultimate whorl (Figure 16) or only slightly expanded and strongly protruding at the periphery.

Type Material: The holotypes of *Toxosoma eboreum* Conrad, 1874 and of *Pseudolacuna macroptera* Boettger, 1878 are adult individuals with broken outer lips; *Liosoma curta* Conrad, 1874 is based on a not fully grown individual with ovoid shape and less pronounced apertural features; no original material was available.

Localities and Material: Pebas Formation, Pliocene: Brazil, Canama (BM(NH) GG 19834/1-3, Etheridge, 1879, here Figure 16); Peru, Iquitos (PIMUZ, numerous spec., de Greve, 1938; here Figure 17 (PIMUZ J/1)); Peru, probably Pichua W of Cochaquinas (BM(NH) GG 19835/1-6: "Amazon Valley, Coll. Mr. Hauxwell. Purch'd 1870"; UPP, holotype of *Pseudolacuna macroptera* Boettger 1878, here Figure 15).

Relationships of the species of *Eubora* and *Toxosoma* and their stratigraphical importance

The different localities yielded different species assemblages of *Eubora* which could be of phylogenetical and thus of stratigraphical importance. The species assemblages are:

Pichua and Pebas: *Eubora crassilabra*, *E. woodwardi*, *E. bella*, *Toxosoma eboreum*.

Iquitos: *Eubora woodwardi*, *E. grevei*, *E. pygmaea*, *Toxosoma eboreum*.

Canama: *Littoridina?* *crassa*, *Toxosoma eboreum*.

Of these faunules, that of Canama is inconclusive, showing only the species *crassa* questionably assigned to *Littoridina*, and *Toxosoma eboreum* which occurs in nearly all localities.

Eubora grevei of Iquitos is very closely allied to *E. bella* of Pichua/Pebas, differing in the weakening of the spiral keels in late ontogenetic stages and—due to the smaller size—by the less pronounced apertural and siphonal (?) characters. Also in *Eubora woodwardi*, the specimens of Iquitos are markedly smaller than those of Pichua/Pebas. Furthermore, *Eubora woodwardi* and *grevei* of Iquitos are rather closely allied (the main difference is the absence resp. presence of spiral keels), while in Pichua/Pebas *E. woodwardi* and *E. bella* (this species is directly allied with *E. grevei*) are clearly separated by their characters.

Thus, the conclusion might be drawn that the fossiliferous beds of Iquitos represent a lower stratigraphical level coinciding with the branching of the keeled and not keeled forms of *Eubora* whereas in the beds of Pichua/Pebas the keeled and not keeled forms are widely separated not only by their sculpture but by their shell dimensions and proportions too (see Figures 1, 2). Moreover, another form (*E. crassilabra*) may be interpreted to have been branched off the *E. woodwardi* stock by adding an additional whorl to the primitive form of *E. woodwardi* (of Iquitos, with small size), increasing more slowly in volume, thus contributing more to the height increase than to the width increase of the shell.

Otherwise, the phylogenetical relations could be interpreted to be inverse, i.e., the fauna of Pebas being ancestral to that of Iquitos, when regarding the early ontogenetic presence of keels in *Eubora grevei*. Assuming the keeled species of *Eubora* evolved from smooth ones, one would expect that the keels made their first appearance in late ontogenetical stages, while a property already developed may vary most strongly in late ontogenetical stages, the early ontogenetical stages remaining more constant. In this case *Eubora grevei* would be interpreted as a form of *E. bella* which has possibly lived under unfavorable conditions, reducing the strength of the spiral ornamentation of the shell as well as its size; the reduction of the size would apply to *E. woodwardi*, too. The beds of Iquitos would then have to be younger or—if lateral facies variation is assumed—of about the same age as the beds of Pichua/Pebas.

This question cannot be answered without knowledge of the relative position of the fossiliferous horizons of Pichua/Pebas and Iquitos; the author can only point to the possibility that a phylogenetical development useful for a stratigraphical subdivision of the Pebas Formation may exist.

The stratigraphical age of the Pebas Formation, however, cannot be assessed by the genera and species treated here, as neither *Eubora* nor *Toxosoma* nor close allies of them have been encountered outside the Pebas Formation.

PALEOECOLOGICAL IMPLICATIONS

The reassessment of the taxonomic position of the genera *Eubora* nom. nov. and *Toxosoma* Conrad, 1874 has consequences for paleoecological interpretations, as the interpretation of the fauna to be of brackish water character was based in part on the attribution of *Eubora* and *Toxosoma* to the marine family Lacunidae. Here *Eubora* and *Toxosoma* are transferred to the Hydrobiidae which include a large number of freshwater and in part brackish water inhabiting species. Also the form described by ETHERIDGE, 1879, under the two names of "*Assimineea crassa*" and "*Hydrobia dubia*" is removed from these genera which indicate littoral marine conditions (*Assimineea*: soft substrates of the supralittoral; *Hydrobia*: littoral to shallow sublittoral and lagoonal habitats, marine to nearly fresh water) and questionably referred to *Littoridina*.

So the brackish water character of the faunas of the Pebas Formation is considerably reduced as now nearly every species of this Formation may occur in fresh water. Apart from *Eubora*, *Toxosoma*, "*Assimineea*" and

"*Hydrobia*", this applies to species of the families Neritidae and Dreissenidae which were often cited to indicate brackish water but may occur as well in fresh water. Only few arguments remain to make slightly brackish conditions probable: 1) The Bivalve genus *Pachydon* Gabb, 1868 belongs to the family Corbulidae otherwise strictly marine, and has been found in Venezuela in brackish water strata (RUTSCH, 1952). It is improbable that this form which evolved from a marine stock migrated into pure fresh water. 2) The faunal associations of the Pebas Formation are not those of typical fresh water, as large groups of fresh water mollusca (Planorbidae, Ampullariidae, Unionacea) are missing or exceptional. 3) Many shells show circular bore holes. Very similar holes are produced by marine gastropods of the families Naticidae and Muricidae. However, as no form assignable to one of these families has been detected, the origin and thus the significance of the holes is unknown.

SUMMARY

Summarizing, the salinity of the depositional environment of the Pebas Formation faunal assemblages was probably near fresh water, possibly oligohaline to miohaline (0.05 to 0.5% salinity).

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